Intraspecific Variation in Growth and Reproduction in Latitudinally Differentiated Populations of the Giant Scallop *Placopecten magellanicus* (Gmelin)

B. A. MACDONALD AND R. J. THOMPSON

Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada

Abstract. The giant scallop, *Placopecten magellanicus*, exhibits a discrete gametogenic cycle which varies between populations. In our study, spawning occurred later in scallops from New Jersey than in those from Newfoundland, but there is no latitudinal trend when data from the literature are considered. Reproduction is probably controlled by local environmental factors.

There was high intraspecific variation in shell and somatic growth rates, and in the production of somatic and germinal tissue. Reproductive output in particular showed great plasticity. Variation in these traits along a depth gradient on a micro-geographical scale was equal to or greater than variation on a latitudinal scale, although reproductive output in New Jersey scallops exceeded that of scallops from Newfoundland. Enhanced reproductive output was associated with reduced longevity.

Introduction

Many species of marine ectotherms are distributed over a wide latitudinal range and often display intraspecific variation in physiological characteristics and life-history strategies (Levinton, 1983). Such species are ideal candidates for determining which environmental factors, such as water temperature, that vary with latitude in a predictable manner may influence the growth and reproduction of individual animals. Causal relationships between water temperature and growth or reproductive output have proved difficult to establish unequivocally, owing to local variations in environmental conditions, such as food availability and temperature (Newell *et al.*,

1982; MacDonald and Thompson, 1985a). There is a need for studies in which intraspecific variation on a micro-geographic scale is examined for a number of characters and related to observations on latitudinally separated populations.

With some exceptions, the general consensus in the literature is that bivalve molluscs from low latitudes grow more rapidly at ambient temperature, attain a smaller maximum size, and have a shorter lifespan than do conspecifics from higher latitudes (Newell, 1964). This view is supported by studies on several species of bivalves, including *Siliqua patula* (Weymouth *et al.*, 1931) and *Mytilus edulis* (Seed, 1976), but clear latitudinal trends have not been observed in others, *e.g., Mya arenaria* (Brousseau, 1979) and *Placopecten magellanicus* (Posgay, 1979). In *Macoma balthica* from North America, however, maximum size is greatest in populations from low latitudes, whereas in *M. balthica* from Europe growth is faster at intermediate latitudes (Gilbert, 1973; Bachelet, 1980; Beukema and Meehan, 1985).

There is an extensive literature on the gametogenic cycle and the timing of spawning in many bivalve species (Giese and Pearse, 1974; Sastry, 1979; Newell *et al.*, 1982). For several species in the northern hemisphere, spawning occurs at higher temperatures and later in the year in southern populations than in northern ones (Sastry, 1970, 1979; Seed, 1976; Barber and Blake, 1983), and is often more synchronized at higher latitudes (Ockelmann, 1958; Bricelj *et al.*, 1987). Unfortunately, there is very little information on intraspecific variation in reproductive output and reproductive effort in latitudinally separated populations (Bricelj *et al.*, 1987), yet these quantities are often more sensitive to environmental change than is shell growth, the most commonly measured variable (MacDonald and Thompson, 1985a, b).

The giant scallop *Placopecten magellanicus* is found only in the northwest Atlantic, between the Strait of Belle Isle, Newfoundland, and Cape Hatteras, North Carolina (Posgay, 1957; Porter, 1974). In previous papers, we have described how local variations in temperature and food supply can influence shell growth, somatic production, gametogenesis, and reproductive characteristics in populations from Newfoundland (MacDonald and Thompson, 1985a, b, 1986; MacDonald *et al.*, 1987). In this paper, we integrate this information with data from scallop populations in New Brunswick and New Jersey, to further our knowledge of intraspecific variation in *P. magellanicus*. The objectives are to establish whether growth and reproductive parameters show identifiable latitudinal trends, to determine which ones should be regarded as plastic or variable on a local scale, and to understand the possible adaptive value of the observed strategies.

Materials and Methods

Study sites and environmental data

Scallops were collected from Sunnyside (47°51′ N, 53°55′ W) in Trinity Bay, Newfoundland, by SCUBA divers, from St. Andrews (45°04′N, 67°04′W) in Passamaquoddy Bay, New Brunswick, and from a bed near Asbury Park (40°13′N, 73°47′W), New Jersey, (Fig. 1) using a modified Digby dredge. Collections were made approximately monthly between July 1982 and November 1983 at Sunnyside and New Jersey for determination of the gametogenic cycle. In 1983 a complete size range of scallops was obtained in the months immediately before and after spawning at Sunnyside (July/September), St. Andrews (July/November), and New Jersey (September/November), to measure the weight loss of the gonad on spawning. Samples were obtained from depths of 10 and 31 m in Sunnyside and St. Andrews but were only available from 31 m at the New Jersey site.

Seasonal water temperatures were recorded in Sunnyside using moored 180 d continuous recording thermographs (Ryan Instruments, Seattle, Washington) and in New Jersey by means of a maximum-minimum thermometer. Temperature cycles for St. Andrews were obtained from Forgeron (1959) and represent mean values for the 1957 and 1958 seasons combined. An approximation for water temperature at 10 m was calculated by averaging the temperature at the surface and the bottom (24 m).

Growth rates

Ages of individual scallops were estimated by interpreting external growth rings on the shell (Stevenson and Dickie, 1954) and growth increments on the calcareous portion of the ligament (Merrill *et al.*, 1966). Measure-
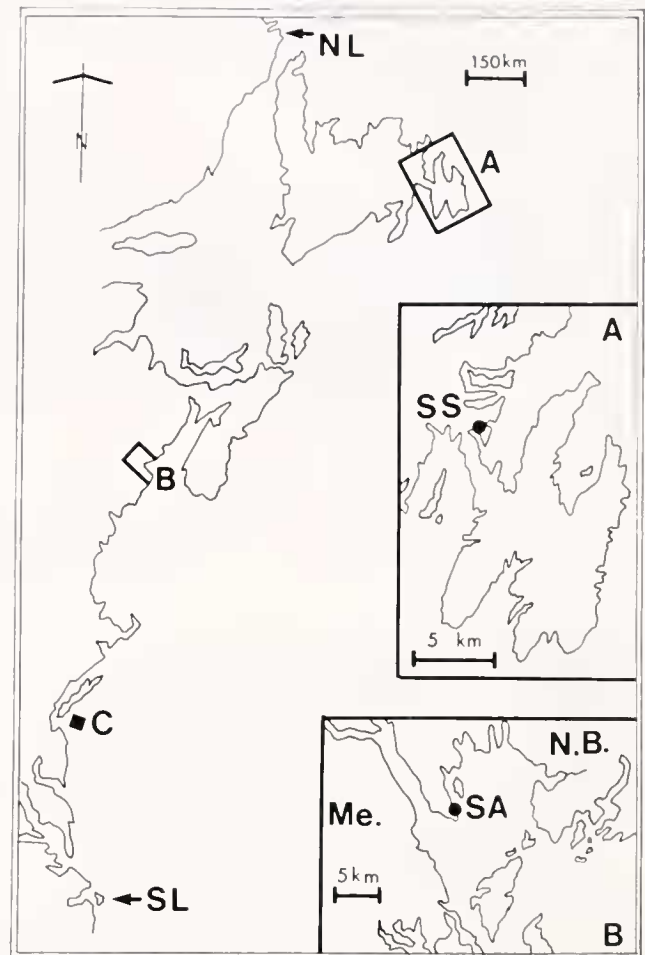

Figure 1. Sites from which scallops, *Placopecten magellanicus*, were collected. A—Avalon Peninsula, Newfoundland (SS = Sunnyside); B—Passamaquoddy Bay (SA = St. Andrews); C—New Jersey. Nl.—northern limit of distribution. SL—southern limit of distribution.

ments of shell height [maximum distance between the dorsal (hinge) and ventral margin (Seed, 1980)] were recorded to the nearest 0.1 mm using vernier calipers. Mean shell heights for each age class were estimated using the von Bertalanffy equation:

$$H_t = H\infty[1 - e^{-K(t-t_0)}]$$

where H_t = shell height at time t, $H\infty$ = mean asymptotic shell height, K = the Brody growth coefficient and t_0 = a parameter representing time when shell height equals zero. The von Bertalanffy functions were fitted by iteration, using the Marquardt algorithm available in the NLIN procedure of the Statistical Analysis System (SAS Institute Inc.).

Weights of the gonad and remaining (somatic) tissue were determined separately for individual scallops after drying at 90°C for 48 h. The mean somatic weight for

each age class was estimated using polynomial regression, which has some advantages over the von Bertalanffy function for describing somatic growth rates (MacDonald and Thompson, 1985a). Polynomial regression, which was computed by the General Linear Model (GLM) procedure of SAS, may be described by the following equation:

$$y = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3 \cdots \beta_m x^m + \epsilon$$

where $\beta_0, \beta_1 \cdots \beta_m$ = population parameters, y = the predicted somatic weight for a given value of x (age) and ϵ = random error at observation x. Linear correlation between regressors (multicollinearity) was reduced by replacing values of x with $(x - \bar{x})$ (Neter et al., 1983).

For predictive and comparative purposes, relationships between shell height and somatic or gonad weight were fitted by SAS (GLM procedure) to the allometric equation $y = ax^b$, where y is the predicted weight (g) at a given shell height x (mm), and a and b are fitted parameters. A linear form of this equation was obtained by transforming both variates to logarithms and fitting the data to a straight line by least squares regression. Owing to possible seasonal differences in shell and somatic growth rates, only those scallops collected from Sunnyside and New Jersey between July and December were used in comparisons with St. Andrews. Statistical comparisons between scallops from the three locations were only made on those individuals collected in 1983 ranging in age from two to eight years because these were the only age classes common to all three populations.

Gametogenic cycle and gamete volume fraction

To establish the gametogenic cycle, histological sections were prepared from the gonads of six male and six female scallops in each monthly sample from Sunnyside (10 m depth) and New Jersey. The proportions of the gonad occupied by developing gametes and mature gametes (the volume fractions) were estimated by a stereological procedure (Lowe et al., 1982). The gamete volume fraction (GVF) was calculated as the sum of the values for developing and mature gametes (for details see MacDonald and Thompson, 1986).

Production

Somatic tissue production (Pg) was calculated from the increments in dry tissue weight between consecutive year classes, assuming that 1 g dry weight = 24.5 kJ (Thompson, 1977). Since *Placopecten magellanicus* has a discrete reproductive cycle and spawns only once a year, gamete production (Pr) was estimated from the weight loss of the gonad on spawning in scallops of given age (determined from the von Bertalanffy equation describing shell height as a function of age), and then con-

verting to units of energy (1 g dry gametes = 26.0 kJ; MacDonald and Thompson, 1985b). Data from males and females were combined, because there were no consistent differences between the sexes in somatic or gonad growth curves (MacDonald and Thompson, 1985b).

Reproductive effort

Reproductive effort (RE), defined as the proportion of non-respired assimilation allocated to reproduction, was calculated for each age class:

$$RE = [Pr/(Pg + Pr)] \cdot 100$$

To compensate for differences in growth rate between populations, RE was also expressed as a function of somatic weight (MacDonald et al., 1987). Furthermore, there were differences in longevity between populations (MacDonald and Thompson 1985a; this paper), so we also related RE to the proportion of the lifespan represented by any given age.

Results
Water temperature

Water temperatures were higher off New Jersey than at the more northerly sites, except in the summer, when the water at St. Andrews was warmer than elsewhere (Fig. 2). In New Jersey, the temperature reached 17°C in November, but never fell below 5°C during the winter, whereas at St. Andrews and particularly at Sunnyside, winter temperatures were much lower. The form of the temperature cycle was similar at St. Andrews and Sunnyside. Water temperatures in the shallower depths at these two locations generally exceeded those in deeper water, except during the winter (December–April), when the water columns were vertically mixed. Cumulative annual day degrees were estimated as 3180 for New Jersey, 2536 (10 m) and 2400 (31 m) for St. Andrews, and 1451 (10 m) and 957 (31 m) for Sunnyside.

Gametogenic cycle

Gametes observed in histological sections were divided into two categories: (1) developing gametes (DG), representing early stages, and (2) mature or ripe gametes (MG), (MacDonald and Thompson, 1986). Since the gametogenic cycles of Sunnyside scallops from 10 m and 31 m were similar (MacDonald and Thompson, 1986), only data from 10 m were used in comparisons with New Jersey scallops.

In both populations (Sunnyside and New Jersey), the seasonal cycles for GVF (TG; males and females combined) were very similar, although in both years Sunnyside scallops spawned two months earlier than those from New Jersey (Fig. 3). According to Dickie (1953)
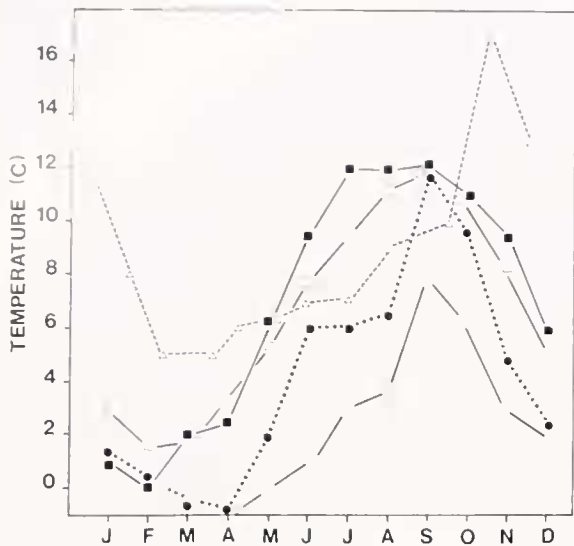
Figure 2. Water temperatures. ● · · ● Sunnyside (10 m); ○---○ Sunnyside (31 m); ■---■ St. Andrews (10 m); □---□ St. Andrews (31 m); △---△ New Jersey.

and Beninger (1987), spawning in *Placopecten magellanicus* from the St. Andrews area occurs at the same time as it does at Sunnyside, *i.e.*, late August to early September. Whereas gametogenesis began earlier in the year at Sunnyside than at New Jersey, mature (ripe) gametes did not appear in Sunnyside scallops until April, compared with January for New Jersey scallops in which mature gametes were present almost year-round. There was a small decrease in GVF (MG) during June and July in scallops from New Jersey, followed by an increase in August, which may suggest partial or dribble spawning (Newell *et al.*, 1982).

Shell growth

Von Bertalanffy equations were used to relate shell height to age for all age classes represented in each sample (Table I). There was a latitudinal gradient in longevity (Sunnyside > St. Andrews > New Jersey; see legend to Table I), although there was no clear trend for asymptotic height ($H\infty$). Shell height was greatest at Sunnyside (10 m) and least at New Jersey, with intermediate values in scallops from St. Andrews, but in deeper water (31 m) at Sunnyside $H\infty$ was relatively small. The Brody growth coefficient (K) was lower in the Sunnyside population (especially at 31 m) than in the others, indicating that scallops from Sunnyside reached asymptotic height relatively slowly compared with those from more southerly locations, but caution must be exercised in comparing growth coefficients when $H\infty$ values are different (see Discussion).

For a rigorous comparison of growth rates, polynomial

regressions afford the advantage that they can be handled by linear models (MacDonald and Thompson, 1985a). Comparisons were made between scallops from 31 m at Sunnyside, St. Andrews, and New Jersey, and also between scallops from the shallowest depths from which they were obtained at each location, using data for individuals two to eight years old (Fig. 4, Table II). Scallops from 31 m at New Jersey and St. Andrews grew at similar rates but significantly faster than scallops from 31 m at Sunnyside. However, when scallops from the shallowest collection depths were compared, shell growth was similar at all three sites.

Somatic weight

Polynomial regressions of somatic weight against age were also compared (Fig. 5, Table II). For scallops from
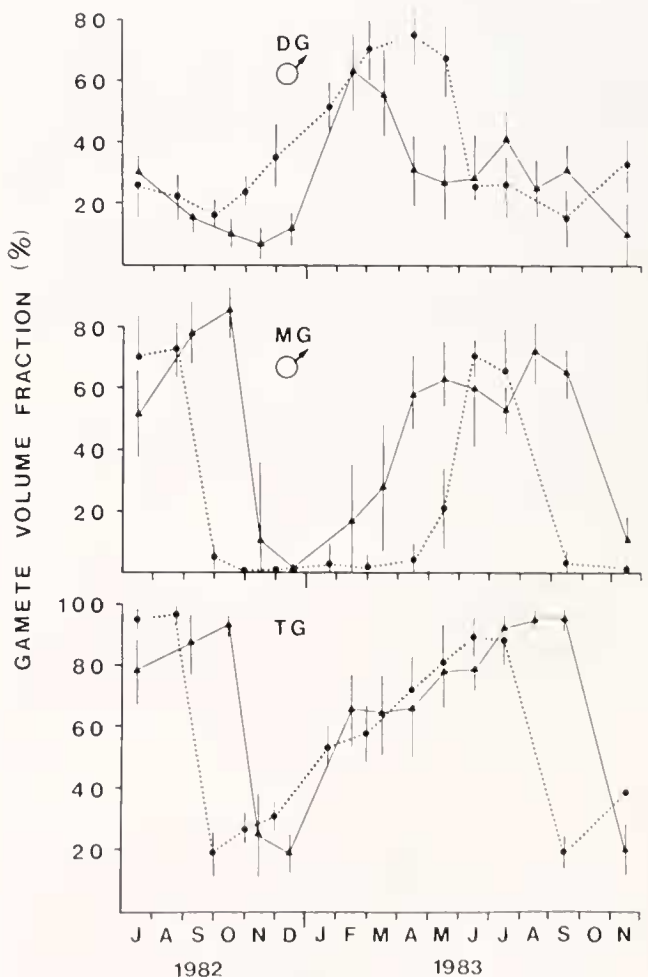

Figure 3. Gamete volume fraction for scallops, *Placopecten magellanicus*, from Sunnyside (10 m depth; ● · · ●) and New Jersey (▲---▲). Data for developing gametes (DG) and mature gametes (MG) are for males only, whereas data for total gametes (TG) are for males and females combined. Values are means ± 95% confidence limits.

Table I

Parameters (± 95% C.L.) of the von Bertalanffy equations describing shell height (H, mm) as a function of age (years) in Placopecten magellanicus *collected from depths of 10 m and 31 m in three locations*

	Sunnyside, Newfoundland		St. Andrews, New Brunswick		New Jersey	
	10 m	31 m	10 m	31 m	10 m	31 m
H_∞	176.5 ± 3.0	158.4 ± 3.3	166.9 ± 12.5	166.0 ± 8.1	—	155.9 ± 9.6
K	0.19 ± 0.013	0.16 ± 0.015	0.21 ± 0.033	0.21 ± 0.032	—	0.22 ± 0.04
t_0	0.55	0.10	0.51	0.53	—	0.32
r^2	0.97	0.97	0.96	0.98	—	0.95
n	272	243	83	73	—	145

The age classes found were 1–20 years at Sunnyside, 1–12 years at St. Andrews, and 1–10 years at New Jersey. r^2 = coefficient of determination, n = number of observations.

31 m, all regressions were significantly different, somatic weight being greatest at St. Andrews and least at Sunnyside. However, at the shallowest depths somatic weight was greater in scallops from St. Andrews and Sunnyside than in those from New Jersey. Significant differences were also observed between linear regressions of somatic weight against shell height (both variates transformed to logarithms), excepting the samples from the shallowest collections at Sunnyside and New Jersey (Tables II, III).

Production

There was a clear latitudinal trend in gamete production (Pr) by individual scallops from 31 m depth (New Jersey > St. Andrews > Sunnyside) which was also reflected in total production (Pg + Pr), but the greatest somatic production (Pg) was at St. Andrews and the least at Sunnyside (Fig. 6). Scallops from New Jersey also pro-

duced more gametes than those from shallow water (10 m) at the more northerly locations, and older individuals from New Jersey (>5 years) showed greater total production. For scallops from the shallowest depths at each site, Pg increased at higher latitudes (Sunnyside 10 m > St. Andrews > New Jersey), although the lowest values for Pg were observed in samples from 31 m at Sunnyside. All comparisons of gonad dry weight at any given shell height showed significant differences between populations, excepting that between Sunnyside (10 m) and New Jersey (Table II).
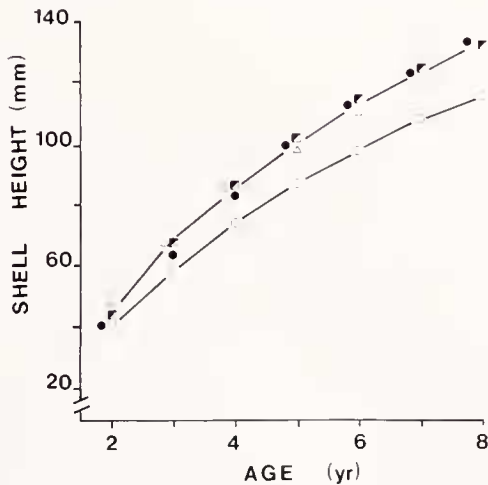

Figure 4. Shell growth in scallops, *Placopecten magellanicus,* from Sunnyside (● 10 m; ○ 31 m), St. Andrews (■ 10 m; □ 31 m) and New Jersey (△).
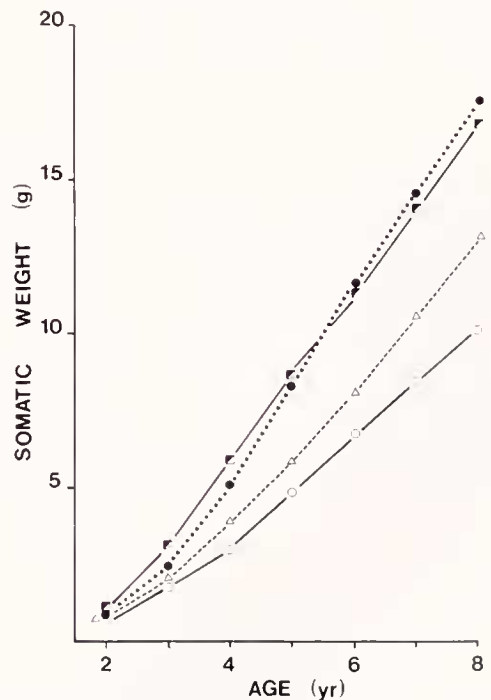
Figure 5. Somatic growth (dry tissue less gonad and shell) in *Placopecten magellanicus* from Sunnyside (●···● 10 m; ○---○ 31 m), St. Andrews (■---■ 10 m; □---□ 31 m), and New Jersey (△---△).

Table II

Summary of (a) t values for comparisons of polynomial regression equations (shell height and somatic weight against age) and (b) comparisons of allometric relationships between somatic weight, gonad weight, and shell height for populations of Placopecten magellanicus

| | | 31 m vs 31 m vs 31 m | | | 10 m vs 31 m⁺ vs 10 m | | |
		NF vs NJ	NJ vs NB	NF vs NB	NF vs NJ	NJ vs NB	NF vs NB
(a) Polynomial t values							
Shell	β_0	5.05***	0.69	4.11***	0.85	0.32	1.59
Height	β_1	4.37***	0.44	4.82***	1.41	0.58	1.12
vs.	β_2	0.70	0.73	0.10	1.13	1.33	0.10
age	β_3	1.84	1.29	0.88	0.87	1.31	0.39
Somatic	β_0	3.58***	4.51***	7.71***	4.29***	7.06***	3.67***
Weight	β_1	3.06**	1.22	5.47***	2.05	2.71**	0.73
vs.							
age	β_2	0.99	0.63	0.55	0.57	0.62	0.02
(b) Allometric regression t values							
Somatic	log a	2.71**	11.10***	—	8.96***	10.12***	0.67
Weight							
vs.							
Shell	b	0.59	1.54	2.48*	1.15	0.12	1.53
Height							
Gonad	log a	—	8.00***	—	2.32	6.52***	—
Weight							
vs.							
Shell	b	4.88***	0.45	5.64***	0.35	2.22	
Height							2.54*

Samples were collected from New Jersey (NJ; 31 m), St. Andrews, New Brunswick (NB; 10 and 31 m), and Sunnyside, Newfoundland (NF; 10 and 31 m). (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, + indicates NJ sample).

The large reproductive output and low body weight of New Jersey scallops resulted in a higher turnover ratio [production: biomass ratio, (Pr & Pg)/B] than in individ-

Table III

Allometric relationships between tissue weight and shell height in Placopecten magellanicus *collected in 1983 from depths of 10 m and 31 m in three locations*

| | Sunnyside, Newfoundland | | St. Andrews, New Brunswick | | New Jersey | |
	10 m	31 m	10 m	31 m	10 m	31 m
Somatic						
log a	−4.67	−3.76	−4.77	−4.55	—	−4.94
b	2.77	2.28	2.83	2.72	—	2.86
r^2	0.97	0.83	0.99	0.99	—	0.93
n	93	97	83	75	—	48
Gonad						
log a	−6.29	−5.75	−9.96	−8.21	—	−7.89
b	3.29	2.87	5.05	4.16	—	4.18
r^2	0.83	0.60	0.92	0.93	—	0.95
n	41	48	43	41	—	24

Regressions are of the form $W = aH^b$, where W = dry weight (g) of the somatic tissue or of the gonad immediately before spawning, H = shell height (mm), a and b are fitted parameters.

uals from the other populations (Fig. 7). At Sunnyside, production per unit weight was greater at 10 m than at 31 m, whereas at St. Andrews the turnover ratio for scallops less than 6 years old was independent of depth. With the exception of the New Jersey population, turnover ratio was a decreasing function of age.

Reproductive effort

There was considerable variation in RE between sites and between depths (Fig. 8). For all ages and sizes, RE at any given age or somatic weight was greatest in scallops from New Jersey, owing to higher Pr and lower Pg values than in individuals from the other populations. At Sunnyside, scallops from 10 m had a greater RE than those from 31 m. Reproductive effort was greater in young scallops (<5 years) from Sunnyside than in those from similar depths at St. Andrews, but lower in scallops older than 5 years. However, when expressed as a function of lifespan, RE was greatest in Sunnyside scallops and least in those from St. Andrews (Sunnyside 10 m > Sunnyside 31 m > New Jersey > St. Andrews 10 m > St. Andrews 31 m), *i.e.*, the maximum values observed for RE were in large, old individuals from the Newfoundland location.
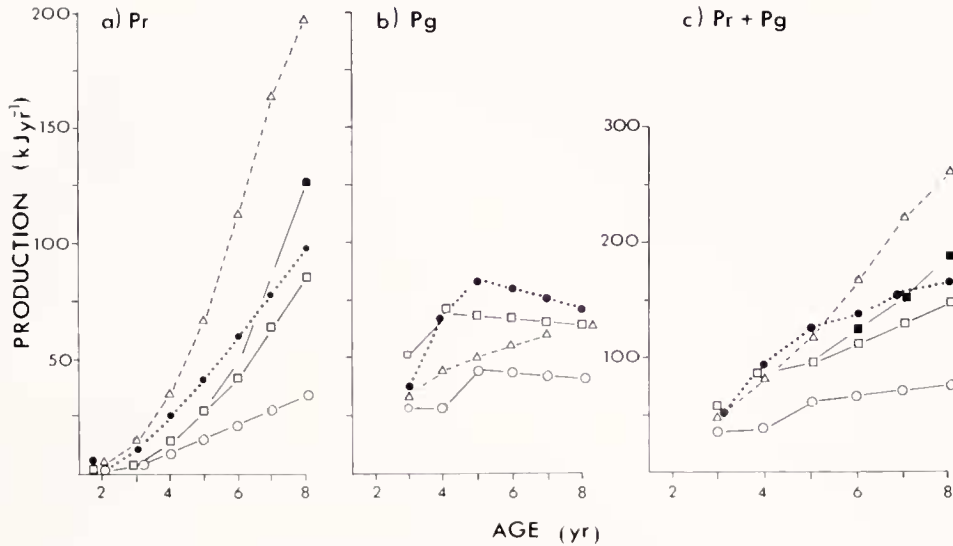
Figure 6. Gonad production (P_r), somatic production (P_g) and total production ($P_g + P_r$) by individual scallops, *Placopecten magellanicus*, from Sunnyside (● · · ● 10 m; ○---○ 31 m), St. Andrews (■---■ 10 m; □---□ 31 m), and New Jersey (△---△).

Discussion

In all the populations of *Placopecten magellanicus* examined here and in others described elsewhere (Thompson, 1977; Robinson *et al.*, 1981; Beninger, 1987) there is a discrete annual reproductive cycle with a well-synchronized spawning period. A slight decrease in GVF in New Jersey scallops during June and July may represent a minor spawning of the type described by Naidu (1970) for scallops from a bed in western Newfoundland, but we did not observe this phenomenon in Sunnyside scallops. In Newfoundland, scallops spawn in August–September (Naidu, 1970; this study). Beninger (1987) and Robinson *et al.* (1981) report a similar timing in *P. magellanicus* from the Bay of Fundy and from Maine, respectively. Our observation that the giant scallop spawns later in the year off the coast of New Jersey suggests that this species may be similar to the bay scallop *Argopecten irradians*, in which spawning occurs later in southern populations than in those further north (Sastry, 1970; Barber and Blake, 1983). Sastry (1970) attributed this latitudinal differentiation in the gametogenic cycle of *A. irradians* to differences in food supply, since the peak in phytoplankton availability occurs later at the southern location than the northern one. However, according to some reports, *P. magellanicus* spawns early (July) at the southern limit of its range (MacKenzie, 1979). On the north shore of the Gulf of St. Lawrence, which is close to the northern limit, spawning also takes place in July (Gaudet, pers. comm.). Thus, there are no clearly identifiable latitudinal trends in the timing of spawning, although the variation appears to be less than in some

other bivalves, notably *Mytilus edulis*, in which the gametogenic cycle may be highly variable over a small geographic range (Lowe *et al.*, 1982; Newell *et al.*, 1982). Borrero (1987) found that the temporal variation across the intertidal zone in the reproductive cycle of the ribbed mussel *Geukensia demissa* may exceed that among latitudinally separated populations. As in other species, re-
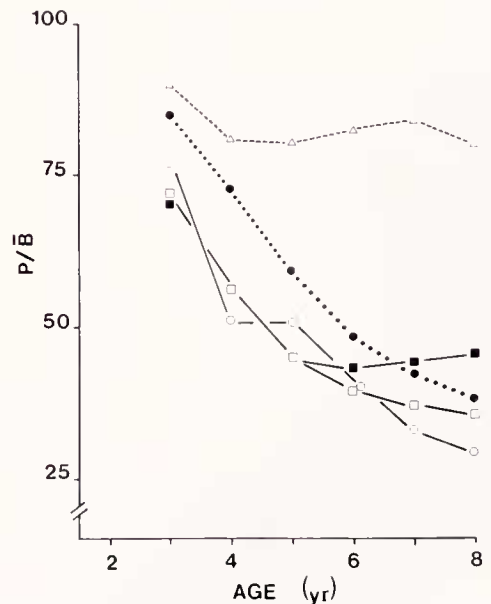

Figure 7. Turnover ratios (production: biomass P/B, where P = P_g + P_r) in scallops, *Placopecten magellanicus*, from Sunnyside (● · · ● 10 m; ○---○ 31 m), St. Andrews (■---■ 10 m; □---□ 31 m), and New Jersey (△---△).
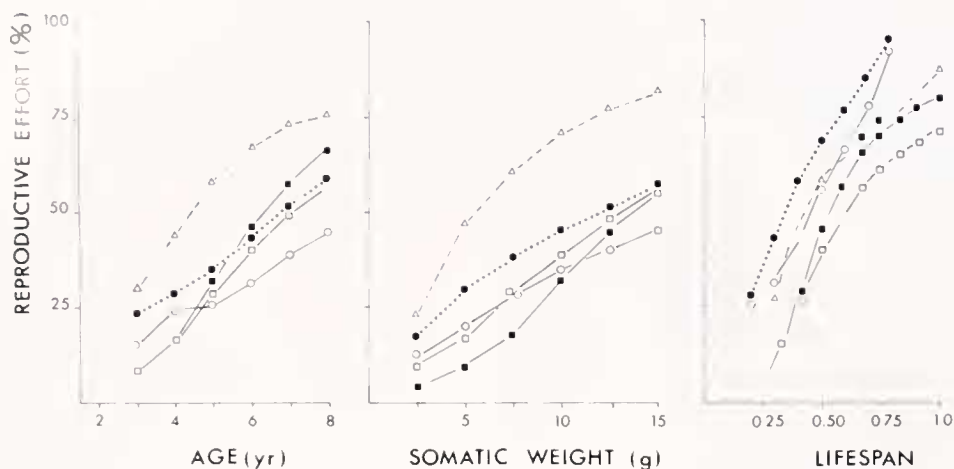
Figure 8.   Reproductive effort, $100 \times P_r/(P_g + P_r)$, as a function of age, somatic weight and lifespan in the scallop *Placopecten magellanicus*. ●··● Sunnyside (10 m); ○---○ Sunnyside (31 m); ■---■ St. Andrews (10 m); □---□ St. Andrews (31 m); △---△ New Jersey.

production in *P. magellanicus* is probably controlled primarily by local environmental factors, especially food supply, which determines the nutrient reserve and hence the capability to initiate gamete development (Newell *et al.*, 1982).

Comparisons of shell growth rates from our own study and others show that differences in shell height at any given age in scallops from Newfoundland, New Brunswick, and Georges Bank are small (Fig. 9), and that there is as much variation between depths at several sites in eastern Newfoundland (MacDonald and Thompson, 1985a) as there is between populations at different latitudes. We have some evidence for an increase in asymptotic height in *Placopecten magellanicus* at higher latitudes, which is consistent with studies on some bivalve species, but not others (see Introduction). However, there is a clear differentiation in longevity, which is greater in northern than in southern populations.

Care must be taken when comparing shell growth rates from different populations, especially when the von Bertalanffy function is used. It is not appropriate to base comparisons on the parameter K when the asymptotic heights or lengths differ considerably between populations, because K is inversely related to $H\infty$ (Ralph and Maxwell, 1977; Haukioja and Hakala, 1979). Furthermore, K is a growth coefficient and should not be regarded as a growth rate *per se* (Ricker, 1975). Attempts to combine $H\infty$ and K into a single parameter have been made (Galluci and Quinn, 1979; Appeldoorn, 1983), but this does not overcome the fundamental problem that the two are interdependent (Beukema and Meehan, 1985). Many of the literature values for von Bertalanffy parameters are of limited value for comparative purposes, since confidence limits are often not provided,

but several statistical packages (including SAS) now include algorithms for handling nonlinear functions of the von Bertalanffy type and provide not only estimates of the parameters but also their variances. We circumvented the problems inherent in the von Bertalanffy function by also fitting polynomials to the shell growth data, which demonstrated that growth was slower at Sunnyside (especially at 31 m depth) than at more southerly
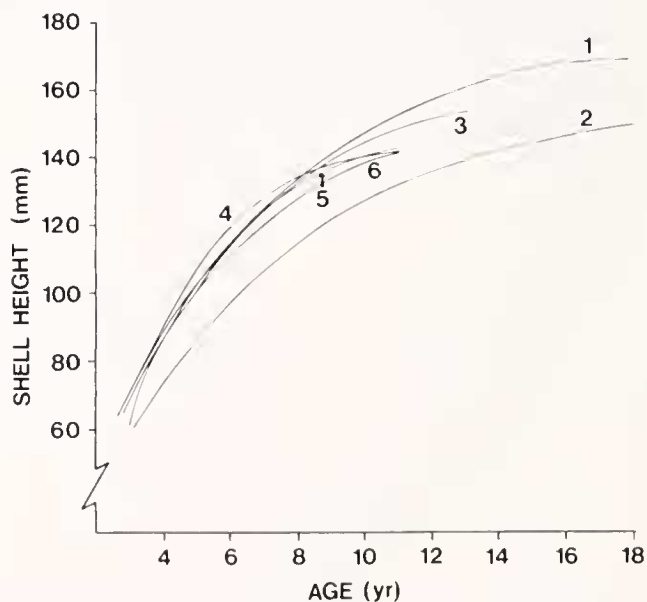

Figure 9.   Shell growth curves for scallops, *Placopecten magellanicus*, from several locations. 1 = Sunnyside, Newfoundland, 10 m depth; 2 = Sunnyside, 31 m; 3 = St. Andrews, New Brunswick (all from MacDonald and Thompson, 1985a); 4 = Georges Bank (Brown *et al.*, 1972); 5 = Mid-Atlantic Bight (Serchuk *et al.*, 1982); 6 = New Jersey (this paper).

locations, but the problem with this approach is that the coefficients themselves have no biological significance.

There is considerable intraspecific variation in the somatic growth rate of *Placopecten magellanicus*, and in the production of somatic and germinal tissue, but only in reproductive output is there any evidence of latitudinal differentiation; scallops from New Jersey are more fecund than those from locations further north. For the most part, variation along a depth gradient on a microgeographic scale may be as great or greater than variation on a latitudinal scale (MacDonald and Thompson, 1985a, b; this study). Reproductive output in particular shows great plasticity, *viz.* the variation between years in shallow water at Sunnyside. Furthermore, MacDonald (1986) recorded greater shell growth rates, reproductive output, and somatic production in giant scallops maintained in suspended culture than in those growing on the bottom nearby.

These findings are consistent with observations on other bivalve species. In a comparison of several populations of *Argopecten irradians*, Bricelj *et al.* (1987) found the greatest differences in fecundity, timing of spawning, adductor muscle weight, and shell height to be between locations less than 2 km apart. In the weathervane scallop, *Patinopecten caurinus*, individuals from offshore beds show slower shell growth, a reduced asymptotic height and lower somatic and germinal production than is found in conspecifics from inshore areas, where food is more plentiful (MacDonald and Bourne, 1987). The growth of shell and somatic tissue is enhanced in the scallop *Chlamys islandica* by growing the animals in suspended culture (Wallace and Reinsnes, 1985). The mussel *Mytilus edulis* also exhibits considerable phenotypic variation in reproductive characteristics over a small geographic range (Bayne *et al.*, 1983). Similar observations have been made on fish (Kipling and Frost, 1969; Mann *et al.*, 1984).

According to Calow (1979), selection for enhanced reproductive output should result in a reduction in the lifespan, and there is a considerable body of evidence to support this position. Thus, in *Placopecten magellanicus*, the shift in emphasis from growth to reproduction occurs earlier in scallops from New Jersey than in those from more northerly locations, and total production is greater in the former than the latter, whereas longevity is reduced in these productive, fecund individuals from New Jersey. Further evidence comes from our observations on scallops from various depths at Sunnyside, Newfoundland. Since we were unable to resolve accurately growth lines for animals older than twenty years, these individuals were excluded from our analyses. However, we did record that a greater proportion (25%) of the total number of scallops (426) taken from 31 m depth fell into this category, compared with only 8.6% (n = 431) at 10

m. Thus on this extremely small geographic scale, longevity is reduced when food and temperature conditions are favorable and production (somatic and gonadal) by individual scallops is increased. Furthermore, MacDonald (1986) has demonstrated that asymptotic height decreases in *Placopecten magellanicus* grown in suspended culture, which is associated with greater production; and in a review of data from several species of limpets, Grahame and Branch (1985) describe a trend whereby longevity is a decreasing, non-linear function of reproductive output and of the growth coefficient K.

The importance of water temperature in determining geographic differentiation in growth rate and fecundity has been emphasized by Levinton (1983) and Lonsdale and Levinton (1985). The latitudinal variation in longevity which we have recorded in *Placopecten magellanicus* is certainly correlated with an observed temperature gradient, and at the Sunnyside site there is also an increase in longevity (associated with decreased production) in scallops from deeper, colder water.

There is little information on the degree to which intraspecific variation in growth and reproduction is environmentally induced or genetically determined. Levinton (1983) identified a genetic component to somatic growth differences among latitudinally separated sibling species in a genus of dorvilleid polychaete, and Lonsdale and Levinton (1986) described genetically based differentiation in both growth rate and fecundity along a latitudinal gradient in a harpacticoid copepod. Thompson and Newell (1985) recorded differentiation in the physiological response to high temperature in two latitudinally separated populations of the mussel *Mytilus edulis*, but were unable to determine whether this was genetic or a result of irreversible phenotypic adaptation. In a reciprocal transplant experiment, Widdows *et al.* (1984) found that most of the physiological variation between two populations of *M. edulis* was attributable to environmental rather than to genotypic factors, although acclimatization was not complete and a genetic component may therefore have been present. This is consistent with other observations on *M. edulis* demonstrating that most of the variation in tissue growth is accounted for by site rather than by stock (Mallet *et al.*, 1987). However, in another study in which reciprocal transplants were made between populations of *M. edulis*, Dickie *et al.* (1984) found a large environmental influence on growth combined with a significant genetic effect.

We have no information on genetic control of growth and reproduction in *Placopecten magellanicus*, but the considerable phenotypic plasticity in this species on a microgeographic scale suggests a strong environmental influence, especially since we have correlated changes in growth and reproduction with temperature and food conditions. This does not necessarily imply that local ge-

netic variability is of no importance, since genetic differentiation can still be significant when phenotypic variation in growth and reproductive traits is greater than the genetic component. The giant scallop exhibits a growth pattern described by Sebens (1987) as Type 1 indeterminate growth (plastic asymptotic growth), in which the size attained by an individual is largely governed by environmental conditions. Such phenotypic variability for a single species merits consideration in any analysis of the adaptive value of reproductive tactics, but has received little attention (Bayne *et al.*, 1983). In the same vein, Stearns (1976) has cautioned investigators against invoking evolutionary explanations to account for reproductive trends without first eliminating genetic and environmental factors, especially food. We conclude that growth and reproductive traits in *Placopecten magellanicus* are inter-related and highly variable on a temporal as well as a spatial scale, as they probably are in many other bivalve species; that local variability often exceeds variation along a latitudinal gradient; and that enhanced reproductive output is associated with reduced longevity.

Acknowledgments

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